THE METABOLIC RATES AND BODY TEMPERATURES OF BATS [1]

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Bats are among the hibernators—those mammals that pass the winter in a profound physiological state, characterized by: (1) reduction of the body temperature to virtually the ambient temperature, (2) reduction of the metabolic rate to an extremely low level, (3) reduction of other body processes (heart rate, respiratory rate, etc.) to minimal levels. These mammals are properly called heterotherms, for they are essentially poikilothermic when hibernating, but when awake and active maintain roughly constant body temperatures comparable to those of typical homoiotherms. It has long been known that bats reduce body temperature and metabolic rate whenever they become inactive (Hall, 1832). This reduction of metabolic rate would seem to be of great advantage to an animal that must expend such great amounts of energy as bats in flight must require. Pearson (1948) says: "Apparently because of small size and strenuous activities many bats have resorted to a metabolic parsimony of periodically lowered body temperature that allows their expensively gathered fuel to nourish them longer."

Despite the realization among naturalists that this remarkable condition exists in bats, there has never been any thorough study made to measure its dimensions, or to evaluate the possible impact on the lives of bats. The temperature coefficient of oxygen consumption has been studied in isolated tissues, in oxidative enzyme systems, in poikilothermic animals, and in newborn young mammals that have not yet developed the ability to regulate their body temperature. But it has not been possible previously to measure metabolic rate or oxygen consumption over a range of 40° C. in an intact, adult mammal. This paper presents the results of such measurements, made with the little brown bat (*Myotis l. lucifugus*) without subjecting the animals to thermal conditions outside of the range encountered in nature.

The investigation began by asking these questions: (1) To what extent do bats reduce their body temperature and metabolic rate during daily periods of inactivity? (2) Is there an essential physiological difference between this daily occurrence and hibernation? (3) Does this phenomenon separate bats from other hibernators on any physiological grounds? (4) What are the implications of this ability to reduce temperature and metabolism in relation to the life history of bats?

Question 4 will be answered in a later publication, as it is of greater interest in a mammalogical context than in a physiological one. However, the other three questions can be answered to a large degree here.

Materials and Methods

The bats used in this study were *Myotis lucifugus lucifugus* Kerr, the little brown bat. This species is found over much of North America, and is very common. Its habits are better known than those of any other American bat (Griffin, 1940; Wimsatt, 1945; Folk, 1940). It is found in hibernation in caves in north-

Table I

Body temperatures of bats in relation to ambient temperature

Experimental temperature		Bat temperatures		Length of experiment	Rate of temperature change
Water bath	Air in vial	At start	At end		
° C.	° C.	° C.	° C.	min.	° C./min.
1.3	1.3	19.1	1.35	45	−0.39
23.0	23.1	24.7	23.2	30	−0.05
30.2	30.2	36.3	31.2	90	−0.05
37.0	35.5	35.7	37.5	15	+0.11

eastern United States during the winter months. It weighs from 5 to 9 or 10 grams.

The bats used for these measurements were collected at caves in central Pennsylvania in winter, or in a large breeding colony near Ithaca, New York, in summer. Those bats taken in summer could be put into a torpid state even in July, merely by placing them in a refrigerator at 2-4° C. They were not fed during the time of their captivity, but were always kept in hibernation. High humidity was maintained in their quarters in order to minimize loss of water.

Apparatus. The determinations of oxygen consumption were made with a Scholander plastic semi-microrespirometer (Scholander, 1950). This had been modified for the present study by attaching the vials to the bottom so that the bats could hang in normal head downward position. Six bats could be measured at one time in the six separate units of this Lucite apparatus.

The body temperatures of some bats were measured with the bat in a similar-sized chamber. A small incision was made in the skin of the bat's abdomen, and a 30-gauge copper-constantan thermocouple inserted laterally along the body wall. This method of measurement of body temperature has been found to be quite close to the rectal temperature (Vernet and Metcalf, 1948). Reference junctions were in the air of the vial and in the water bath.

Procedure. The bats were removed from the cold box, weighed, and placed in the apparatus after an interval of time which was adjusted insofar as possible so that the bat would be placed into the glass vial with a temperature close to that at which the experiment was to be conducted. The experiments lasted for varying periods of time at the different temperatures, because when first·placed in the chamber, the bat was active and consumed oxygen at a high rate. At 2° and 10° C., the steady state of oxygen consumption was not usually reached until eight hours had passed, while at 20° and higher it was reached much more quickly. At these higher temperatures death rates increased rapidly as the experiment lengthened, perhaps due to rapid depletion of already low nutritive reserves. Thus, the optimum length of the determinations at the various temperatures was selected at some point midway between the average time at which the steady state was reached and the average time of death.

The metabolic rate of interest in this study is obviously that of resting bats at various body temperatures. Hence the values obtained during the initial state of

TABLE II

Averages of oxygen consumption of Myotis l. lucifugus at various ambient temperatures

Ambient temperature	No. of bats	Average weight	Average length of steady state period	Minimum metabolism	Maximum metabolism	Average metabolism
° C.		gms.	hrs.	ml. O_2/gm./hr.	ml. O_2/gm./hr.	ml. O_2/gm./hr.
0.5	5	5.2	2	0.039	0.170	0.113
2.0	21	5.2	25.5	0.022	0.039	0.030
10.0	13	5.9	16	0.049	0.094	0.071
20.0	27	6.2	4.15	0.232	0.555	0.393
30.0	21	7.0	1.12	1.06	2.96	2.00
37.0	12	6.9	1.25	2.00	5.11	2.89
41.5	3	7.0	1.00	3.79	4.66	4.14
44.0	5	6.4	0.5	1.12	1.78	1.47

activity were excluded and the metabolic rates during the declining phase at the end of long experiments were also not considered to be relevant. All data presented below represent average values of oxygen consumption during steady state periods with no visible activity, periods within which the individual determinations of oxygen consumption show no extreme variation and no trend either upward or downward. In Table II is shown the average duration of this steady state period at various temperatures. As might be expected, much longer periods of constant metabolic rate could be obtained at lower temperatures.

EXPERIMENTAL RESULTS

The data collected in this study have been plotted in Figures 1 and 2. In addition, all similar data from the literature have been collected, re-calculated to the present units if necessary and plotted in order to find whether the present data are near to the normal condition. The data on metabolic rate taken from other workers are not shown here.

Body temperatures. A primary point to be established in each measurement was the body temperature of the bat. It would have been difficult to conduct all
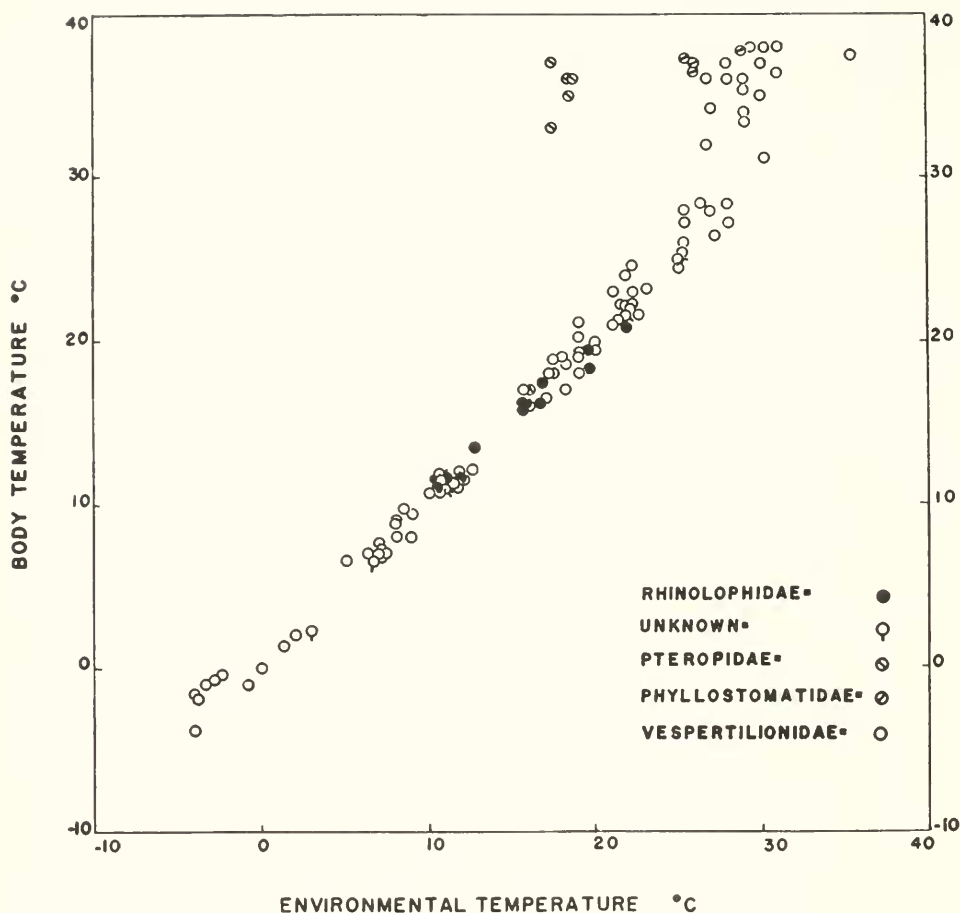
FIGURE 1. Body temperatures of bats in relation to environmental temperature. Data from the present study and all known literature. Four families, ten genera, and nineteen species are included. These are—Vespertilionidae—Hock, *Myotis lucifugus;* Reeder, 1949, *M. californicus;* Eisentraut (1933), *M. myotis, M. natteri, M. mystacinus, M. daubentonii, M. dasycneme, Nyctalus noctula, Eptesicus scrotinus, Pipistrellus nathusii;* Eisentraut (1934), Delseaux (1887), and Kayser (1939), *Plecotus auritus;* Prunelle (1811), *Vespertilo murinus;* Burbank and Young (1934), *Nyctalus noctula;*—Rhinolophidae—Burbank and Young (1934), *Rhinolophus ferrum-equinum, R. hipposideros;* —Pteropidae—Burbank and Young (1934), *Pteropus geddei, P. giganteus, P. cotinus;*—Phyllostomatidae—Wislocki (1933), *Phyllostomus hastatus, Carrollia perspicillatum;*—Unknown—Pembrey and White (1896).

experiments with rectal thermocouples in the animals, particularly at the higher temperatures when the bats were alert and ready to actively struggle against any irritating attachment. Furthermore, a thermocouple attached to the body would undoubtedly have produced an increased metabolic rate in many of the animals. It was therefore decided to determine how closely the body temperature of bats approximated that of the water bath during the steady state period described above.

Accordingly, rectal temperatures were measured by copper-constantan thermo-couples in bats at 4 water bath temperatures ranging from 1.3° to 37.0° C. The results are shown in Table I. It can readily be seen that by the end of the experimental period the rectal temperatures had come to a level closely approximating that of the water bath. The high initial rectal temperature at 1.3° C. bath temperature resulted from the fact that the bat was awake and warm when first placed into the apparatus; after 45 minutes, however, the rectal temperature had fallen to 1.35° C. and it seemed clear that the animal was in a condition comparable to the steady state period of the metabolic rate determinations.

In all cases there was a rapid approximation of the bat's temperature to the air temperature of the vial. This rapidity of change of body temperature increased as the difference between the original body temperature and the ambient temperature
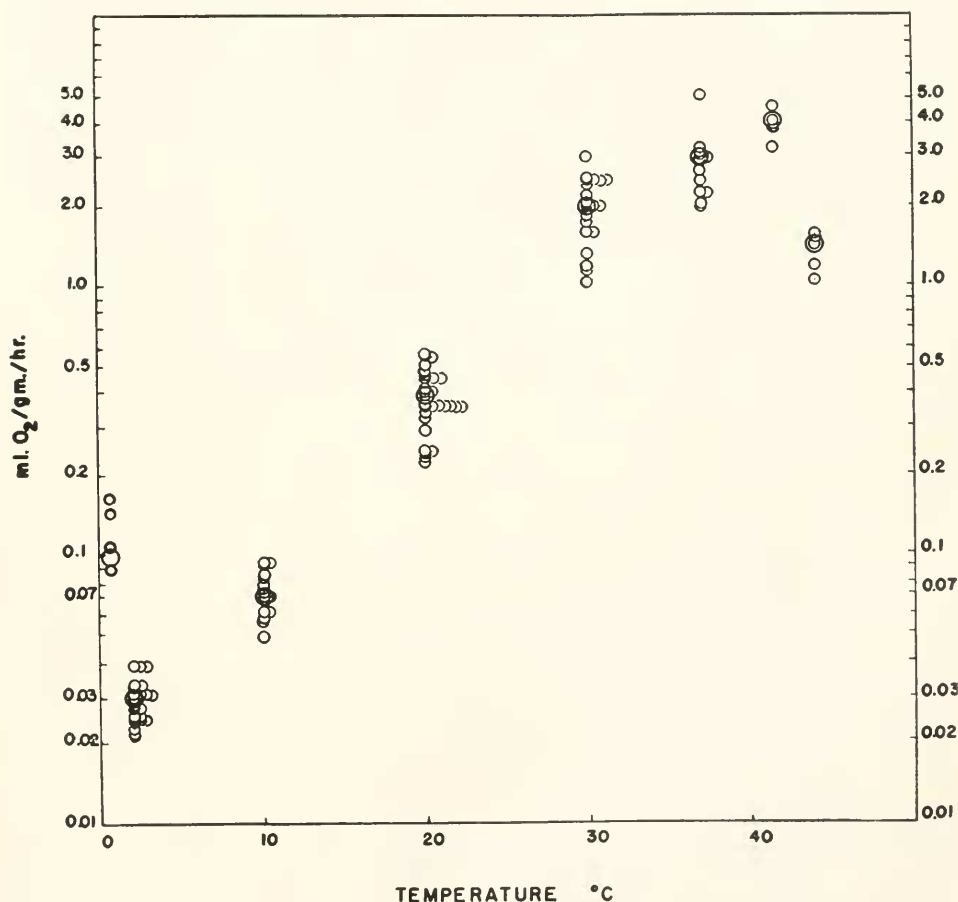

FIGURE 2. Semi-logarithmic plot of the metabolic rates of bats in relation to temperature. The temperature shown is environmental, but is very close to body temperature. Duplicate values are shown at the right of the line. Large circles are the average values.

increased. Table I shows these temperature determinations, including the rates of temperature change. It is apparent that body temperature closely approximates ambient temperature at all levels, but is closer at lower temperatures.

These results are in agreement with virtually all of the available information on body temperatures of bats. For example, Eisentraut (1934) found that the temperature of *resting* bats was nearly identical with the temperature of the surrounding air. Hence, during the steady state period of the present measurements, the body temperatures of the bats were, in all probability, less than 1 or 2° C. above the water bath temperature.

Figure 1 is a plot of all the body temperatures of bats that could be collected from this study and the literature, and that were not ruled out by the presence of activity at the time of the determination. It will be seen that there is an excellent approximation to a straight line. Furthermore, these data relate to several families and many genera of bats, and not only to a small closely related group.

Burbank and Young (1934) studied tropical fruit bats in Oxford zoos, and found that they maintained temperatures higher than that of the environment by means of shivering, flitting the wings, and other muscular activity. *Pteropus* sp. at room temperatures of 20° C. were always awake. At air temperatures of 17.5° to 18.5°, body temperature varied from 33.0° to 37.5° C.

Eisentraut (1938) studied temperature fluctuation in bats of the Cameroons. He found that the temperature at which they passed from a waking state to a lethargic state was *lower* than that found in temperate zone bats. However, he concluded that tropical bats behave in respect to daily reduction of body temperature just like the German bats he had studied. Further, he says, "Zusammenfassend lässt sich also sagen, dass die Beobachtungen an tropischen Fledermäusen gezeigt haben, dass auch sie eine höchst unvollkommene Wärmeregulation besitzen, dass ihre Körpertemperatur und damit ihr Stoffwechsel weitgehend von Umgebungstemperaturen abhängig sind."

It thus appears that all bats exhibit a lack of thermoregulatory control when they become inactive, although they are capable of raising their temperature above that of the environment.

Metabolic rate. It may be expected from the above discussion on body temperature of bats that they will exhibit a variable metabolic rate dependent on the ambient temperatures to which they are subjected. Bats were exposed to ambient temperatures varying from 0.5° to 44.0° C., and their oxygen consumption measured. Figure 2 shows the results of these experiments. Each point represents the average oxygen consumption of one bat for the duration of the steady state period. Table II gives the average of all the steady state metabolic rates at each temperature, and gives also the average length of the period, the number of bats tested, and the average weight of the bats used.

The metabolic rate is at its minimum at 2° C., and is approximately double that value at 10° C. This is the range of temperature which Eisentraut (1934) characterizes as "deep hibernation." At 20° C., metabolic rate is five times that found at 10°, and by 30° there is another five-fold increase. Eisentraut (1934) delimited his "Tageschlaflethargie", or light hibernation as from 10° to 28° C. From 30° to 37° there is a smaller increase (1½ times) reflecting perhaps the fact that the bats are awake at the lower limit, although not yet with a "normal" body temperature. From 37° to 41.5° C., metabolic rate again increases 1½ times. This temperature

was selected for study because it has been stated to be the body temperature during flight (Burbank and Young, 1934). Furthermore, Barkow (1846) found body temperatures of bats when awake to be 41.0° to 41.6° C., although he did not say whether they were flying or not. At 44° C., the metabolic rate was lower than at 41.5°, and death occurred quickly. It thus appears that bats live on a narrow limit of temperature tolerance at the upper level, although there is a very great tolerance at the lower limits. However, the fact that cooling by evaporation could not be accomplished in the vials of the apparatus to the degree possible in the wild must be considered as a possible factor in this rapid death.

At 0.5° C., the metabolic rate quadrupled from that found at 2°. The bats thus increased metabolic rate as the temperature approached the freezing point, even though they were in deep hibernation. Lyman (1948) found that Syrian hamsters responded to temperatures of −1.5° to 1° C. in three ways; the majority increased oxygen consumption and cheek-pouch temperature, and finally awoke; two hamsters increased oxygen consumption to a steady rate 3–4 times that recorded before ambient temperature was reduced, and maintained a cheek-pouch temperature 1.7° to 3.4° C. above that of the environment for as long as 22 hours; four animals died in hibernation, perhaps due to poor condition of the animals. Note that these are the three possible reactions of hibernators to temperatures below 0° C.: to awake, to increase metabolic rate and body temperature without awaking, or to die.

Johnson (1929) subjected ground squirrels to temperatures near freezing and found that in many cases they awoke, and then returned to hibernation at these low temperatures. Some squirrels did not awake, however, but died when the temperature was at or below 0° C. Wyss (1932) found that dormice showed a great increase in metabolism below 0° C., while the body temperature was at least 2° above freezing. Dubois (1896) and Benedict and Lee (1938) reported conflicting results with marmots. Dubois states that they *always* awoke when subjected to near zero temperatures, while Benedict and Lee say that near zero temperatures *never* awakened their marmots.

Unfortunately, the experiment with bats at 0.5° was not continued long enough to show whether or not the bats would have awakened. One of the five bats tested did not increase its metabolism above the range of values found at 2°, while all others went much beyond this. It may be that these four would have awakened in time, while the one that did not increase metabolic rate would have died. It is interesting to note that Eisentraut (1934) has recorded body temperatures of bats as low as −3° C. Kalabuchov (1933) subjected bats to temperatures of −5° to −17° C., and reported that if freezing did not reach the vital organs (lungs, heart, etc.) the bats could be revived by thawing. It would be desirable to know the metabolic rates of bats under such conditions.

Discussion

Comparison with other data on bats. Metabolic rates of bats have been determined by several authors, either as oxygen consumption (Almeida *et al.*, 1926; Kayser, 1938, 1939, 1940; Morrison, 1948; Pearson, 1947), or carbon dioxide production (Delseaux, 1887; Koeninck, 1899; Pembrey and White, 1896), or both (Burbank and Young, 1934; Hari, 1909). These have been measured over a small range of temperatures with the exception of the series by Kayser (1940). The

range covered in his study is from 4° to 30° C. This is a study of *Nyctalus* (*Vesperugo*) *noctula,* and although the number of determinations at any one temperature is small, the study is comparable to the present series of measurements. (Kayser's series on *Pipistrellus* covers a range from 5° to 17° C., and contains more figures at each temperature. There is, however, such great variation that it cannot have involved resting bats in all cases. At 5°, for example, oxygen consumption varies as much as 150:1). I have not used Kayser's mean figures, because it seems that he excluded some data that are admissible from the point of view of my study.

When the data for *Nyctalus noctula* (Kayser, 1940) are compared with those for *Myotis lucifugus* as ml. O_2/gm./hr., very close correspondence is found at the lower temperatures (2° and 4°, 10° and 12.5° C.). At 20° there is a fair correspondence between the two series, but at 30° the rate for *M. lucifugus* is four times that found for *N. noctula.* Two explanations seem possible: (1) the sample used by Kayser was too small, and does not represent the average metabolism; or (2) there is indeed a difference in the metabolic rate in the two species. The latter possibility seems to be the more likely, for my *minimum* metabolic rate was higher than Kayser's maximum (not included in calculations). Further, it is well known that the metabolism of animals (of the same general type, *e.g.,* mammals) varies inversely with increased size, whether plotted as weight or as surface area. *N. noctula* is three to four times larger than *M. lucifugus,* and calculations from the mouse-to-elephant curve of Benedict (1938) indicate that the difference in the metabolic rates of these two species at 30° is not far from the expected divergence for their weight variation. It may, however, be significant that no difference could be detected in metabolic rate per gram at lower temperatures.

Comparison with data on other hibernators. There are many studies of the temperature and metabolism of heterotherms during hibernation and when awake. Dubois (1896) found no fluctuation of the body temperature of marmots and other hibernators except in the fall, immediately preceding hibernation. Johnson (1928), on the other hand, states that ground squirrels (*Citellus* sp.) showed temperature fluctuation at all times of the year. When not hibernating the range of temperature was 32° to 41° C. The lower temperatures graded into those of slight torpor at about 29° to 32° C. Johnson (1931) considered that these fluctuations of body temperature in response to changes of ambient temperature were due (in part, at least) to the animal's "rather poorly adjusted heat regulating mechanism." Hamilton (1934) observed that the body temperatures of nine woodchucks varied from 34.9° to 40.0°, with the average 37.4° C. It thus appears that there is a lability of the body temperature of these heterotherms which extends over a small range, even when the mammal is not hibernating.

Kayser (1939) studied the effect of variations in ambient temperature upon the respiratory exchange of hibernators when they were awake. He used hedgehog, hamsters, marmot, spermophile, and dormice, as well as bats. All of these animals, with the exception of the bats, were capable of thermoregulation, although not to the same degree of precision as that found in the homoiotherms. Kayser also found that the basal metabolism of hibernators when awake was not distinctly different from that of the homoiothermic mammals.

Conclusions. It is now proper to sum up the evidence offered, in an attempt to answer the questions posed in the introduction. First, it is evident that bats can greatly reduce metabolic rate and body temperature. However, the normal daily

reduction has not been indicated thus far. The answer seems to be that these physiological measures of energy production are reduced to a level dictated by the ambient temperature. For a bat resting in 20° C., therefore, body temperature will be close to 20°, and metabolic rate will be near that indicated in Figure 2 for that temperature. This will be true at *any* ambient temperature, as long as the bat is in a resting state.

Question 2 asked whether there was a physiological difference between hibernation and the daily reduction of body temperature and metabolic rate. Hall (1832) called this latter state "diurnation," in contrast to "hibernation." Eisentraut (1934) called it "Tageschlaflethargie," or "leichter Lethargie," in contrast to "Winterschlaf" or "tief Lethargie," and considered that 10° C. was the dividing line between these two states. It does not seem to me that there is any essential distinction between them, and that those differences that do exist are those of degree, not of kind. To be sure, metabolic rate is greatly increased during exposure to temperatures above 10°, but this alone does not warrant erection of a new state, or the dignity of a new term. Rather it appears that the increased metabolism at these intermediate temperatures is a reflection of the increased function of tissues and organs of the bat, although it is still not capable of locomotion. In this respect, bats may be compared to the frogs, toads, and curarized dog of Krogh (1914), all of which showed an increase in metabolism at 20° although no movement occurred. To summarize, no basic physiological distinction can be shown to exist between the conditions found during the daily sleep of bats and those found during hibernation.

It seems apparent that the heterothermic mammals (other than bats) when not hibernating have physiological characteristics much like those of their non-hibernating relatives. Body temperature varies over a greater range, and metabolism reflects this, but both are in nearly all respects closely similar to the phenomena manifested by homoiotherms. Bats differ from other heterotherms in that their body temperature when at rest *at any season* always approximates that of their environment. The metabolic rate reflects this change, so that the metabolism is in direct proportion to the body temperature at all times. This condition is in opposition to that found in homoiotherms, where metabolism varies with external temperature, while body temperature remains nearly constant. Even other hibernators do not exhibit this phenomenon, for their metabolic rate does not vary in relation to body temperature when they are not hibernating. Rather, the metabolic rates during hibernation are of a quite different magnitude than those found during the normal state, and only these levels are clearly demonstrable, for when passing into or out of hibernation the metabolic rate at any one body or ambient temperature is a transitory affair (Lyman, 1948). Bats are thus the only mammals in which metabolic rate varies directly with body temperature. Question 3 must then be answered to the effect that bats are much different from other heterotherms in their lack of thermoregulation at all times of the year.

Summary

1. Oxygen consumption was measured in resting little brown bats, *Myotis l. lucifugus*, at ambient temperatures from 0.5° to 44.0° C. Body temperature was shown to approximate the ambient level under the conditions of the experiments, so

that in effect the metabolic rate was measured over very nearly this range of body temperatures.

2. The function relating oxygen consumption to body temperature is not linear; the Q_{10} is 2.94 from 2° to 10° C., 5.54 from 10° to 20° C., 5.09 from 20° to 30° C., 1.69 from 30° to 37° C., and 2.22 from 37° to 41.5° C. The ratio between highest and lowest resting metabolic rates is 138:1; the temperatures represented are 41.5° and 2° C.

3. Some notes on the reaction to temperatures very close to 0° C. are included. Bats increased metabolism over that observed at 2° C. when exposed to near-freezing temperatures. The experiment was not continued long enough to find whether or not they would eventually awake.

4. The data are compared with the findings of other investigators using several species of bats. There is a close correspondence between body temperature and ambient temperature in all species, except that the tropical forms increase heat production by muscular work. Bats of the temperate zone appear to show the usual effect of size on metabolic rate per unit weight at temperatures of 30° C. or above, as Benedict (1938) has demonstrated occurs in a wide variety of homoiotherms. At 2° and at 10° C. this difference is not apparent in a comparison between these measurements and those made by Kayser (1940) on a much larger bat.

5. It is concluded that there is no physiological basis for distinguishing the daily reduction of temperature and metabolic rate in bats from that found in hibernation, except in degree. It appears that this daily phenomenon is due to a lack of thermoregulatory control.

6. Bats are considered as distinct from other heterotherms in that, at all seasons of the year, their resting temperature and metabolic rate is dependent on the ambient temperature. This also is due to their lack of thermoregulation. They are the only mammals in which the resting metabolism is a direct function of the body temperature, rather than of the ambient temperature. Nevertheless, when active, they can maintain body temperatures of 40° C. or above.

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